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A response to Pennisi - "How do gut microbiomes help herbivores", a hint into next-generation biocontrol solutions

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Abstract

In a world where invasive invertebrate species can significantly compromise food security and where a dwindling range of synthetic pesticides remains our principal line of defence, testing a new invasion ecology hypothesis and understanding what makes a phytophagous insect invasive should be regarded as high priority research. Recent advances in microbiology strongly support the crucial and effective role of the gut microbiome in insect growth, development and, most importantly, environmental adaptation to their host plants. On the basis of recent literature, and following Elizabeth Pennisi's article published in the journal *Science*, we hypothesis that gut microbiome could be a critical determinant of invasion success in phytophagous insects, and that the uncovering of common traits in the gut microbiome of invasive insects, a "gut microbiome invasiveness signature", would open new avenues of research towards next-generation biocontrol solutions.

Keywords

Pest, invasive species, phytophagous insects, bacteria, biological control

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INTRODUCTION

In her in depth News Story published on the 20th of January issue of Science (p236), Elizabeth Pennisi asked the striking and yet challenging question: "*How do gut microbiomes help herbivores?*". While Pennissi mentioned the capacity of woodrats to consume otherwise lethal plants because of the specificity of their gut microbiome, the letter mainly enumerated and discussed a number of examples in insects, where gut microbiome contributes to breaking down and recycling waste compounds and other plants toxins. However, none of the examples reported were that of an invasive or a pest species. Despite this, we believe that the study of the gut microbiome opens fascinating new research avenues in the fields of basic and applied invasion ecology, where scientists work at understanding the determinants of insect invasion success and devising new ways to control these damaging species. Since Elton's theories in invasion ecology (Elton 1958), and those reviewed by Simberloff and Rejmanek in their encyclopaedia (2011), very few novel theories have been proposed to explain the rise and success of invasive phytophagous insects. One unexplored question that directly relates to the research highlighted by Pennisi and which could be the basis of a new invasion ecology hypothesis is: *Could the gut microbiome determine the invasion success of phytophagous insects?*

LITERATURE SUPPORT

There have been calls recently for a better understanding of the role of gut microbiome in invasive species in general (Bahrndorff 2016) and in shaping phytophagous insect diversification and co-evolution with plants (Hammer and Bower 2015), yet few have stressed the significant breakthrough that "a gut microbiome invasiveness signature" in phytophagous insects would represent. In invasive species, dispersal ability, environmental tolerance, phenotypic plasticity and associated epigenetics are critical determinants of invasion success (Simberloff and Rejmánek 2011, Chown et al. 2015). It has already been demonstrated that some of these attributes can be modified through the action of gut bacteria (e.g. Kim et al. 2016). Furthermore, we know that numerous plant defence compounds, such as monoterpenes, diterpenes, phenolics and alkaloids can be metabolized by bacteria (Malecky et al. 2012, Marmulla and Harder 2014, Hammer and Bowers 2015, Vilanova et al. 2016), and crucially, some invasive insects seem able to tolerate (Piskorski et al. 2011) and even benefit (Lefort et al. 2015) from such compounds. The presence of gut microbial communities capable of metabolising plant defence compounds (Chung et al. 2017) could explain why some phytophagous insects are invasive whilst others are not. Several studies have already clearly stressed the central role of insect gut microbiome in overcoming the plant toxin barriers to facilitate insect host shifts (e.g. Tsuchida et al. 2004, Hammer and Bowers 2015). It is also known that host shifts can sometimes lead to a phytophagous insect becoming an invasive species (Lefort et al. 2014).

The metabolising of plant defence compounds by gut bacteria could also explain the intraspecific variation in the level of invasiveness of some species observed between

different regions (e.g. biotype/ecotypes) such as in the whitefly *Bemisia tabaci* (Gennadius) (De Barro et al. 2006), where climate does not appear to be the controlling factor. Furthermore, because the different components of gut microbes can either be horizontally or vertically transmitted (Engel and Moran 2013), this could result in variation in composition between regions where limited gene flow might occur.

For all the above reasons, we believe that it is extremely important to further investigate the "gut microbial facilitation hypothesis" proposed by Hammer and Bowers (2015), and to give it a new dimension that also encompasses the role of the gut microbiome in phytophagous insect invasion success. A better understanding of the mode of transmission of microbes involved in detoxification or metabolisation of plant defence compounds is also essential in future research.

OUTCOMES AND IMPORTANT CONSIDERATIONS

The human population will reach over 9 billion people by 2015, and international trade and climate change continue to drive increasing introductions of invasive phytophagous insects (Bradshaw et al. 2016, Seebens et al. 2017). This presents an extreme challenge to modern agriculture and requires a significant shift towards sustainable practices that can meet the demand for food whilst limiting harmful effects on the environment. In particular, broad-range synthetic pesticides and chemical fertilisers need to be phased out in favour of better-targeted biological control strategies (Porter et al. 2009; Godfray and Garnett 2014). Uncovering a "gut microbiome invasiveness signature" could lead to improved risk assessments following the incursions of new phytophagous insects but, more importantly, it would open new avenues of research towards next-generation biocontrol solutions. In a study by Ceja-Navarro et al. (2015), gut microbiome disruption by antibiotic treatment in coffee berry borers (*Hypothenemus hampei* (Ferrari)), resulted in the loss of the insect ability to degrade caffeine, a purine alkaloid that plays a key role in plant defences against phytophagous insects (Ashihara and Crozier 2001). Should a gut microbiome invasiveness signature be confirmed in invasive phytophagous insects, new strategies targeting bacterial symbionts of interest, rather than the invasive insect itself, and adapted to their mode of transmission, could be developed. Such solutions would have broad range effects across invasive phytophagous insects but no harmful effects on non-invasive and/or beneficial insects. Important considerations to guaranty the applicability and success of such a solution include distinguishing between the core "invasion" microbiome (i.e. the invasiveness signature) and the core "functional" microbiome (i.e. microbial regulation of other host physiologies/behaviours). It will also be necessary to fully understand the functional redundancy of the microbiome in invasive phytophagous insects to avoid functional compensation of the disrupted invasive traits. Finally, thoroughly testing the solutions in the field will be required as it has been previously shown that responses of hosts to "microbiome engineering" are not necessarily long-lasting (Sheth et al. 2016), and unexpected variation in hosts/environmental conditions might occur.

AUTHOR CONTRIBUTION

MCL, SB and TR developed the concept, MCL designed and wrote the manuscript, SB and TR revised the manuscript. MCL 60%, SB 20%, TR 20%.

Authors	Contribution	ACI
MCL	0.60	3
SB	0.20	0.50
TG	0.20	0.50

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REFERENCES

Ashihara H, Crozier A (2001) Caffeine: a well known but little mentioned compound in plant science. Trends in Plant Science 6(9): 407–413. https://doi.org/10.1016/S1360-1385(01)02055-6

Bahrndorff S, Alemu T, Alemneh T, Lund Nielsen J (2016) The microbiome of animals: implications for conservation biology. International Journal of Genomics 2016: 5304028. https://doi.org/10.1155/2016/5304028

Bradshaw CJ, Leroy B, Bellard C, Roiz D, Albert C, Fournier A, Barbet-Massin M, Salles JM, Simard F, Courchamp F (2016) Massive yet grossly underestimated global costs of invasive insects. Nature Communications 2016(7): 12986. https://doi.org/10.1038/ncomms12986

Ceja-Navarro JA, Vega FE, Karaoz U, Hao Z, Jenkins S, Lim HC et al. (2015) Gut microbiota mediate caffeine detoxification in the primary insect pest of coffee. Nature Communications, 6: 7618. https://doi.org/10.1038/ncomms8618

Chown SL, Hodgins KA, Griffin PC, Oakeshott JG, Byrne M, Hoffmann AA (2015) Biological invasions, climate change and genomics. Evolutionary Applications 8(1): 23–46. https://doi.org/10.1111/eva.12234

Chung SH, Scully ED, Peiffer M, Geib SM, Rosa C, Hoover K, Felton GW (2017) Host plant species determines symbiotic bacterial community mediating suppression of plant defenses. Scientific Reports 7: 39690. https://doi.org/10.1038/srep39690

De Barro PJ, Bourne A, Khan SA, Brancatini VAL (2006) Host plant and biotype density interactions–their role in the establishment of the invasive B biotype of *Bemisia tabaci*. Biological Invasions 8(2): 287–294. https://doi.org/10.1007/s10530-005-1261-6

Elton CS (1958) The ecology of invasions by animals and plants. London, Methuen. https://doi.org/10.1007/978-1-4899-7214-9

Engel P, Moran NA (2013) The gut microbiota of insects–diversity in structure and function. FEMS Microbiology Reviews 37(5): 699–735. https://doi.org/10.1111/1574-6976.12025

Godfray CHJ, Garnett T (2014) Food security and sustainable intensification Philosophical Transactions of the Royal Society 369: 6–11.

Hammer TJ, Bowers MD (2015) Gut microbes may facilitate insect herbivory of chemically defended plants. Oecologia 179: 1–14. https://doi.org/10.1007/s00442-015-3327-1

Kim D, Thairu MW, Hansen AK (2016) Novel Insights into Insect-Microbe Interactions-Role of Epigenomics and Small RNAs. Frontiers in Plant Science 7: 1164. https://doi.org/10.3389/fpls.2016.01164

Lefort M-C, Boyer S, De Romans S, Glare T, Armstrong K, Worner S (2014) Invasion success of a scarab beetle within its native range: host range expansion versus host-shift. PeerJ 2: e262. https://doi.org/10.7717/peerj.262

Lefort M-C, Worner SP, Rostas M, Vereijsen J, Boyer S (2015) Responding positively to plant defences, a candidate key trait for invasion success in phytophagous insects. New Zealand Journal of Ecology 39: 128–132.

Malecky M, Albarello H, Broudiscou LP (2012) Degradation of terpenes and terpenoids from Mediterranean rangelands by mixed rumen bacteria *in vitro*. International Journal of Animal Bioscience 6(4): 612–6. https://doi.org/10.1017/S1751731111001947

Marmulla R, Harder J (2014) Microbial monoterpene transformations-a review. Frontiers in Microbiology 5: 1–14. https://doi.org/10.3389/fmicb.2014.00346

Pennisi E (2017) How do gut microbes help herbivores? Counting the ways. Science 355: 236. https://doi.org/10.1126/science.355.6322.236

Piskorski R, Ineichen S, Dorn S (2011) Ability of the oriental fruit moth *Grapholita molesta* (Lepidoptera: Tortricidae) to detoxify juglone, the main secondary metabolite of the non-host plant walnut. Journal of Chemical Ecology 37(10): 1110. https://doi.org/10.1007/s10886-011-0015-4

Porter J, Costanza R, Sandhu H, Sigsgaard L, Wratten S (2009) The value of producing food, energy, and ecosystem services within an agro-ecosystem. Ambio 38: 186–93. https://doi.org/10.1579/0044-7447-38.4.186

Seebens H, Blackburn TM, Dyer EE, Genovesi P, Hulme PE, Jeschke JM, et al (2017) No saturation in the accumulation of alien species worldwide. Nature communications 8: 14435.

Sheth RU, Cabral V, Chen SP, Wang HH (2016) Manipulating bacterial communities by in situ microbiome engineering. Trends in Genetics 32(4): 189–200. https://doi.org/10.1016/j.tig.2016.01.005

Simberloff D, Rejmánek M (2011) Encyclopedia of biological invasions (No. 3). University of California Press.

Tsuchida T, Koga R, Fukatsu T (2004) Host plant specialization governed by facultative symbiont. Science 303: 1989–1989. https://doi.org/10.1126/science.1094611

Vilanova C, Baixeras J, Latorre A, Porcar M (2016) The generalist inside the specialist: Gut bacterial communities of two insect species feeding on toxic plants are dominated by *Enterococcus* sp. Frontiers in Microbiology, 7:1005. https://doi.org/10.3389/fmicb.2016.01005